

***Monadelpha* (Euphorbiaceae, Plukenetieae), a new genus of Tragiinae from the Amazon rainforest of Venezuela and Brazil**

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Abstract

Monadelpha L.J.Gillespie & Card.-McTeag., **gen. nov.**, is described as a new member of Euphorbiaceae tribe Plukenetieae subtribe Tragiinae, to accommodate *Tragia guayanensis*, a species known from western Amazonas, Venezuela and, newly reported here, from Amazonas, Brazil. The genus is unique in the subtribe for having 5-colpate pollen and staminate flowers with filaments entirely connate into an elongate, cylindrical staminal column terminated by a tight cluster of anthers. Phylogenetic analyses based on nuclear rDNA ITS and sampling 156 accessions across the diversity of Tragiinae (all 12 genera and 77 of ~195 species) also support *Monadelpha* as a distinct lineage that is separate from *Tragia*. A revised key to the genera of Tragiinae in South America and Central America is provided.

Keywords

Brazil, ITS, molecular phylogeny, Plukenetieae, pollen, *Tragia*, Venezuela

Introduction

Members of tribe Plukenetieae are morphologically unusual within Euphorbiaceae for frequently possessing stinging hairs, twining vine or liana habit, and colorful pseudanthia (in *Dalechampia*). The tribe is characterized by apetalous flowers, valvate staminate

sepals, and undivided styles that are basally to entirely connate. Plukenetieae contains three subtribes (i.e., Dalechampiinae, Plukenetiinae, Tragiinae), of which Tragiinae is the largest and most diverse, with 12 genera and ~195 species as currently circumscribed (Webster 2014; with updates by Medeiros et al. 2013; Cardinal-McTeague and Gillespie 2016) (Table 1). Subtribe Tragiinae is distinguished from Plukenetiinae by stinging hairs and consistently 3-locular ovaries and eglandular leaves, and from Dalechampiinae by racemose or thyrsoid inflorescences rather than bibracteate pseudanthia (Gillespie 1994a; Webster 2014).

Among Tragiinae, the most species-rich genus is *Tragia*, which includes ~150 species, whereas the other 11 genera are much smaller with only one to 11 species each (Table 1). The complex infrageneric classification of *Tragia* currently comprises two subgenera, six sections (including sect. *Monadelphae* L.J.Gillespie), one species group, and two unplaced species (Table 1). A single species has been segregated as *T.* subg. *Mauroya* (Leandri 1971); however, our preliminary research suggests this species is closely allied with sect. *Agirta* and does not warrant subgeneric status. All other species belong to *T.* subg. *Tragia*. Three other sections, sects. *Leptorhachis* (Klotzsch) Müll. Arg., *Leucandra* (Klotzsch) Müll.Arg. and *Ratiga* Müll.Arg., that are sometimes considered distinct are included here within sect. *Tragia*, a position supported by pollen (Gillespie 1994a) and molecular studies (Cardinal-McTeague and Gillespie 2016). *Tragia* species exhibit very diverse pollen and floral morphology that is correlated in part with its infrageneric classification (Gillespie 1994a, b). The genus was suggested to be highly paraphyletic based on this morphological diversity (Gillespie 1994a), which is confirmed by recent molecular phylogenetic studies focused on Plukenetieae (Cardinal-McTeague and Gillespie 2016). Three sections of *Tragia*, sects. *Bia* (Klotzsch) Müll. Arg., *Ctenomeria* (Harv.) Benth., and *Zuckertia* (Baill.) Müll.Arg., were recently reinstated as genera (Webster 2007, 2014; Medeiros et al. 2013) based on inferences from pollen morphology (Gillespie 1994a), floral morphology, and preliminary molecular results (Wurdack et al. 2005), and are supported by our more in-depth molecular study (Cardinal-McTeague and Gillespie 2016).

One of the most unusual species of *Tragia* is *T. guayanensis* L.J.Gillespie, which was considered so distinct as to merit its own monotypic section, *Monadelphae* L.J.Gillespie (Gillespie 1994b). The species is characterized by two features unique in Tragiinae: 5-colpate pollen and filaments entirely connate into an elongate cylindrical staminal column (Figs 1, 2). All other *Tragia* species have 3-aperturate pollen, which is mostly 3-colpate, sometimes 3-porate or with three poorly defined apertures (Table 1), with the exception of 4-colpate in *T. rubiginosa* Huft (preliminary observations in Gillespie 1994b), a species unplaced in the sectional classification. Filaments in staminate flowers of *Tragia* are usually distinct to sometimes basally connate. The only other species having filaments entirely connate is *T. lassia* Radcl.-Sm. & Govaerts of sect. *Lassia*, which has stamens connate into a very short disc-like structure (Baillon 1858: pl. 4, figs 24, 25; pers. obs.), and very different from that of *T. guayanensis*. When describing *T. guayanensis*, Gillespie (1994b) suggested the species was distinct and not closely related to any other *Tragia* species. Nevertheless, she maintained the species within

Table 1. Tragiinae genera and infrageneric taxa of *Tragia*: species number, geographic distribution, and pollen morphology. Adapted from Cardinal-McTeague and Gillespie (2016) with pollen characters from Gillespie (1994a, 1994b) and taxonomic updates from this paper.

Genus/section	spp. #	Geographic distribution	Pollen apertures	Pollen tectum
<i>Acidoton</i> Sw.	5	Hispaniola, Jamaica	inaperturate	rugulate
<i>Bia</i> Klotzsch	5	Costa Rica to South America	inaperturate	foveolate-fossulate or finely reticulate
<i>Cnesmone</i> Blume	11	SE Asia	weakly 3-colpate	punctate
<i>Ctenomeria</i> Harv.	2	South Africa	weakly 3-aperturate	finely foveolate-reticulate
<i>Gitara</i> Pax & K.Hoffm.	1	Central and South America	3-colpate	finely foveolate-reticulate
<i>Megistostigma</i> Hook.f.	5	SE Asia	weakly 3-colpate to inaperturate	punctate
<i>Monadelpha</i> L.J.Gillespie & Card.-McTeag., gen. nov.	1	Venezuela (Amazonas), Brazil (Amazonas)	5-colpate	foveolate
<i>Pachystylidium</i> Pax & K.Hoffm.	1	SE Asia	weakly 3-porate	punctate
<i>Platygyne</i> P.Mercier	7	Cuba	inaperturate	reticulate or rugulate
<i>Sphaerostylis</i> Baill.	2	Madagascar	unknown	unknown
<i>Tragia</i> L.	~150	Pantropical to warm temperate		
sect. <i>Agirta</i> Baill.	5	Madagascar	unknown	unknown
sect. <i>Lassia</i> (Baill.) Müll.Arg.	2	Madagascar	3-colpate	reticulate
sect. <i>Leptobotrys</i> (Baill.) Müll.Arg.	2	SE USA	weakly 3-porate	punctate
sect. <i>Tagira</i> Müll.Arg.	82	Africa, Madagascar, S Asia	3-colpate	reticulate
sect. <i>Tragia</i>	53	S USA to South America, Caribbean	3-colpate	intectate-baculate
Australian species group	3	Australia	3-porate	punctate
<i>T. biflora</i> Urb. & Ekman (unplaced)	1	Hispaniola	unknown	unknown
<i>T. rubiginosa</i> Huft (unplaced)	1	Venezuela	4-colpate	punctate
subg. <i>Mauroya</i> Leandri	1	Madagascar	weakly 3-aperturate	finely reticulate
<i>Tragiella</i> Pax & K.Hoffm.	4	E and S Africa	3-colpate	reticulate
<i>Zuckertia</i> Baill.	2	Mexico, Central America	3-colpate	finely reticulate

Tragia in its own section pending further study and anticipating that a major reclassification along phylogenetic lines would be necessary.

Here we present molecular phylogenetic results placing *T. guayanensis* within subtribe Tragiinae that supports its recognition as a distinct genus. The new genus *Monadelpha* is described for *T. guayanensis* based on its unique pollen and floral morphology and isolated phylogenetic position within Tragiinae. This is the first of several contributions towards a new phylogenetic classification of subtribe Tragiinae.

Material and methods

Molecular phylogeny

To determine the phylogenetic relationships of *Monadelpha*, we sequenced and analyzed the Internal Transcribed Spacer (ITS) region (including complete ITS1, 5.8S, and ITS2, and flanking portions of 18S and 26S) of nuclear rDNA. ITS has been

shown to provide good resolution of Tragiinae in the prior studies (e.g., Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019) from which our core taxon sampling is drawn and presents few alignment problems across genera. Orthologous plastid data could not be recovered from the degraded *Monadelpha* sample, but the limited phylogenetic resolution of the more slowly evolving plastid loci is established and their addition would be unlikely to change our findings. Our taxon sampling of 156 accessions included 77 of ~195 species of Tragiinae (39% of total diversity) with representatives of all 12 Tragiinae genera and seven of the eight sections/species groups in *Tragia* (excluding the Madagascan subg. *Mauroya*, only known from its type collection of *T. ivohibeensis* Leandri). Due to unusually high GC content in the close relatives of Tragiinae (which results in challenging DNA alignments and recovers some questionable relationships; Cardinal-McTeague, unpublished data), we rooted the tree using three accessions from the sister clade of Plukenetieae, which contains tribes Bernardieae and Caryodendreae (Wurdack et al. 2005; Cervantes et al. 2016).

Extractions of genomic DNA, fluorescent Sanger sequencing, and contig assembly for the ITS sequences followed the protocols of previous molecular studies in Plukenetieae (Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019). The paratype of *T. guayanensis* (Williams 14990, US) was sampled and sequenced at the Smithsonian separately from all other new data, under more stringent conditions for degraded museum samples following protocols in Dorr et al. (2018). That specimen is well preserved and the data appear authentic based on appropriate negative controls and unique phylogenetic placement. The sequences were aligned using the auto-select algorithm of MAFFT ver. 7.450 (Kato and Standley 2013) in Geneious ver. 11.1.5 (BioMatters, Auckland, New Zealand), and the optimal model of nucleotide evolution was ranked by AIC (Akaike Information Criterion) using default search parameters across three substitution schemes in jModeltest2 ver. 2.1.6 on XSEDE (Darriba et al. 2012; Miller et al. 2010). Subsequent analyses were conducted on all data in the alignment and potentially ambiguous regions were few.

We estimated a phylogenetic tree using Bayesian inference with MrBayes ver. 3.2.6 on XSEDE (Ronquist et al. 2012), executing an (MC)³ analysis with two runs of 3 million generations and sampling every 1000 generations, using the optimal model of nucleotide evolution on an unpartitioned alignment (remaining parameters as default). Runs were considered converged if ESS (effective sample size) of each parameter were >500 in Tracer ver. 1.7 (Rambaut et al. 2018), and if PSRF (potential scale reduction factor) and the standard deviation of split frequencies were close to 1.0 and <0.005, respectively, as determined by the MrBayes output. A 50% majority rule consensus tree was calculated following a 25% burn-in, resulting in Bayesian posterior probability (PP) values based on posterior distribution of 4500 trees from the combined runs. For an additional estimate of branch support, we inferred maximum likelihood bootstrap percentages (MLBP) using 1000 rapid bootstrap replicates under default parameters with RAxML-HPG ver. 8 on XSEDE (Stamatakis 2014). In the Results, we interpret strong branch support as PP >0.95 and MLBP >85. Discussion

of the subclades (T1–T10) follows the naming convention of Cardinal-McTeague and Gillespie (2016) with minor adjustments.

Data resources

The data underpinning the analyses reported in this paper (DNA alignment and resulting Bayesian tree) are deposited in the Dryad Data Repository at <https://doi.org/10.5061/dryad.5hqbzkh4d>.

Morphology

Specimens were examined at CAN and US, on loan from MO, NY, and P (herbarium acronyms following Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>), and from other herbaria via online images in the Global Biodiversity Information Facility (GBIF.org 01 Oct 2020 Occurrence Download <https://doi.org/10.15468/dl.upmgky>). The key was adapted from Gillespie (1994b), modified and updated based on examination of specimens and the following references: Mulgura de Romero and Gutierrez de Sanguinetti (1989); Radcliffe-Smith (2001); Medeiros et al. (2013); Steinmann and Ramírez-Amezcuca (2013); Cardinal-McTeague and Gillespie (2016); Webster (2014).

Phylogenetic results

Our 159-terminal (80 taxa) ITS dataset, including 55 new sequences, had an aligned length of 795 characters (410 variable, 353 parsimony informative [44%], 0.7% missing data), and GTR+I+G was identified as its optimal model of nucleotide evolution. Bayesian and ML analyses revealed very similar results. The 50% majority rule Bayesian topology was well resolved with most clades strongly supported by PP and MLBP (Fig. 3).

The phylogeny is divided into two major clades with strong to moderate support, the Old World Tragiinae clade (T1–T3) and the New World Tragiinae clade (T4–T10). The resolution of subclades T1–T3 was strongly supported, with subclade T1 (*Ctenomeria*) sister to T2 (*Cnesmone*, *Megistostigma*) + T3 (*Tragia* sect. *Tagira*, embedded with *T.* sects. *Agirta* and *Lassia*, and *Tragiella*). Subclades T4–T10 were mostly strongly supported, with the exception of the modified subclade T6/9, which includes the new genus *Monadelpha* with moderate support (PP = 0.92, MLBP = 56). The New World Tragiinae clade contains a small successive grade of subclades T4 (*Bia*) and T5 (*Acido-ton*, *Platygyyna*) that culminates into the strongly supported Core New World Tragiinae clade (T6–T10). This core clade comprises a weakly supported clade (PP = 0.90, MLBP <50) with three distinctive subclades, T6/9 (*Gitara*, *Monadelpha*, and *Zuckertia*) sister to T7 (*Tragia* sect. *Leptobotrys*) + T8 (Australian *Tragia*, *Pachystylidium*, and *Sphaerostylis*), which together are sister to the large subclade T10 (*Tragia* sect. *Tragia*). *Monadelpha* is on a long branch, moderately supported as sister to *Zuckertia* + *Gitara* (PP = 0.92, MLBP = 56), and well separated from *Tragia* and other Tragiinae genera.

Discussion

The phylogenetic relationships of Tragiinae recovered here largely agree with previous phylogenetic analyses of Plukenetieae based on ITS and plastid *psbA-trnH* data (Cardinal-McTeague and Gillespie 2016). Our increased Tragiinae taxon sampling (77 here compared to 50 previously) improved both resolution and support, despite including only ITS data. A noteworthy difference is the revised placement of *Gitara* (subclade T9, formerly weakly supported as sister to *Tragia* sect. *Tragia*, T10; Cardinal-McTeague and Gillespie 2016), which is here strongly supported as sister to *Zuckertia* (T6), with *Monadelpha* sister to both of them. *Monadelpha* is an isolated lineage, clearly distinct from New World and Old World clades of *Tragia*. Support for its relationship with *Gitara* and *Zuckertia* (subclade T6/9) is not strong, which suggests that its position on the phylogeny may not be stable and could vary with additional sequence data. Inclusion of the *Monadelpha* ITS sequence in a broader analysis of Plukenetieae that sampled six loci (nuclear ribosomal ETS, ITS; low copy *KEA1*, *TEB*; plastid *matK*, *ndhF*; results not shown) recovered similar results with strong support for subclade T6/9, the inclusion of *Monadelpha* in subclade T6/9, and with weak support for generic relationships therein (Cardinal-McTeague et al., unpublished).

The 5-colpate pollen of *Monadelpha* is unique among Plukenetieae. All other Plukenetieae have 3-aperturate or inaperturate pollen, with the exception of *T. rubiginosa* (discussed below). Among New World Tragiinae, *Gitara*, *Zuckertia*, and *Tragia* sect. *Tragia* pollen is 3-colpate, whereas pollen of *Acidoton*, *Bia*, and *Platygyne* is inaperturate, and *T.* sect. *Leptobotrys* is 3-porate (Gillespie 1994a, 1994b) (Table 1). *Monadelpha* shares uneven colpus margins with the 3-colpate taxa. Its tectate-foveolate exine is more similar to the tectate and finely fossulate-reticulate or finely reticulate exines of *Gitara* and *Zuckertia* than to the intectate-baculate exine of *Tragia* sect. *Tragia*.

Monadelpha is also morphologically distinct, especially its staminate flowers with filaments completely connate into a long cylindrical staminal column bearing a tight terminal cluster of ± 5 anthers. *Acidoton*, *Bia*, *Gitara*, *Platygyne*, and *Zuckertia* all have numerous free stamens, the large *Tragia* sects. *Tragia* and *Tagira* have 3 stamens (sometimes more, to 22) that are distinct or connate only at the base, and *T.* sect. *Leptobotrys* has two stamens (rarely 3) connate basally. Only the distantly related *Tragia lassia* (*T.* sect. *Lassia*) of Madagascar has stamens or filaments entirely connate, but this feature has obviously evolved independently. Its androecium, consisting of a small 3-anthered disc-shaped structure on a very short narrow column, is very different from that of *Monadelpha*.

Other characters of *Monadelpha* that are unusual for Tragiinae include unisexual inflorescences and long, mostly distinct styles. Whereas most Tragiinae have bisexual inflorescences with pistillate flowers proximal, *Monadelpha* shares unisexual inflorescences with *Gitara* and the Caribbean genera *Acidoton* and *Platygyne* (plus a few species of Old World Tragiinae). Styles of *Monadelpha* are slender, cylindrical, mostly smooth (papillose only at the apex), up to 10 mm long, and connate basally (up to $\frac{1}{4}$ their length). Most New World Tragiinae and Old World *Tragia* have styles that are much shorter, relatively thicker, and basally to mostly connate into a thick stylar

column. Perhaps most similar is *Zuckertia* with somewhat longer (to 5 mm), slender cylindrical styles that are connate into a slender column, but differ in the degree of connation (1/2–3/4 their length) and the free portion papillose adaxially.

Tragia rubiginosa from Amazonian Peru is another morphologically unusual *Tragia* species (Huft 1989) that is unplaced in the present sectional classification. The species has 4-colpate pollen (preliminary observations in Gillespie 1994b) and is the only species in Tragiinae other than *Monadelpha* with a pollen aperture number greater than three. Its broad, thick, subsessile stigmas are unique in Tragiinae and its staminate flowers with five sessile anthers are unusual. The species is morphologically distinct from *Monadelpha*, and the two taxa are unlikely to be closely related. Molecular data is not yet available to determine its phylogenetic position within Tragiinae.

The isolated phylogenetic position (including a long branch length), and accompanying distinctive stamen and pollen morphology all support the recognition of *Monadelpha* as a new genus separate from *Tragia*. Our results suggest a possible relationship with the northern South American and Central American monotypic genus *Gitara* and the Mexican and Central American ditypic genus *Zuckertia*.

Taxonomic treatment

***Monadelpha* L.J.Gillespie & Card.-McTeag., gen. nov.**

urn:lsid:ipni.org:names:77213225-1

Tragia section *Monadelphae* L.J.Gillespie, Novon 4: 331. 1994.

Diagnosis. Similar to *Tragia* and other Tragiinae genera but differing in having 5-colpate pollen and monadelphous stamens with filaments entirely connate into an elongate, cylindrical staminal column with anthers tightly clustered together at apex.

Type and only known species. *Monadelpha guayanensis* (L.J.Gillespie) L.J.Gillespie & Card.-McTeag.

Description. *Habit* climbing vines, apparently monoecious; latex absent; stems twining; stems, leaves and inflorescences with stinging and simple hairs. *Stipules* narrowly triangular or lanceolate, small, caducous. *Leaves* simple, alternate, evergreen, petiolate, eglandular; blades elliptic, ovate-elliptic, broadly elliptic, broadly ovate-elliptic, or suborbicular, chartaceous, apex acuminate, base narrowly cordate, margins irregularly serrulate or denticulate with minute glandular setae, venation pinnate; petiolar and laminar glands absent. *Inflorescences* slender racemes, unisexual, flowers single per node in bract axil; bracts small, lanceolate or narrowly lanceolate, eglandular; staminate inflorescence axillary; pistillate inflorescence (known only in fruiting stage) terminal but appearing leaf-opposed. *Staminate flowers* pedicellate; sepals 5, narrowly oblong, valvate; corolla and disc absent; stamens apparently 5, monadelphous; filaments connate into an elongate, ±cylindrical staminal column, bearing a dense cluster of ±5 anthers; pollen 5-colpate, oblate-spheroidal to suboblate, amb pentagonal, exine

tectate-perforate, tectum foveolate and microverrucate, colpi with uneven margins. *Pistillate flowers* (description based on old flowers on infructescence axis) pedicellate; sepals 6, ovate, distinctly imbricate, margins entire; corolla and disc absent; ovary 3-locular with 1 ovule per locule, 3-lobed, densely covered with stinging hairs; styles 3, long-cylindrical, mostly distinct, connate basally for 10–25% length, papillose at apex. *Fruits* 3-lobed capsules, dehiscent into 3 bivalved mericarps; pericarp woody, sparsely covered with stinging hairs; columella persistent, with 3 perpendicular apical arms; seeds 3, subglobose, abaxial surface somewhat obtusely angular, ecarunculate; sepals persistent.

Etymology. The genus name is combined from *monos* (Greek, one) and *adelphos* (Greek, brother), and refers to monadelphous with filaments united and to *Tragia* section *Monadelphae*.

***Monadelphha guayanensis* (L.J.Gillespie) L.J.Gillespie & Card.-McTeag., comb. nov.**

urn:lsid:ipni.org:names:77213226-1

Figures 1, 2

Tragia guayanensis L.J.Gillespie, Novon 4: 330–338. 1994.

Type. VENEZUELA. Amazonas: Río Casiquiare entre la boca del [Río] Siapa y el caño Momoni, 18 Feb–4 Mar 1986, B. Stergios & G. Aymard 9182 (holotype: MO-260419! – staminate; isotype: NY-00076710! – pistillate).

Description. See Gillespie (1994b). Emended here (based on *Ule* 5013): *Leaves*: petiole 2–8 cm long, blade elliptic, ovate-elliptic, broadly elliptic, broadly ovate-elliptic, or suborbicular, 12–25 × 6–17 cm, apex with acumen 1–2 cm long, base cordate with narrow sinus 0.8–2.5 cm deep, margins irregularly serrulate or denticulate. *Staminate inflorescences* ~3–18 cm long.

Etymology. The specific epithet is derived from Guayana, and refers both to the Guayana Shield region of northern South America and to the Guayana Region of Venezuela where the species is native. Guayana is of Amerindian derivation by European colonists, and may come from the tribe Guayanos or the Indigenous word *uayana*, meaning pale (see Berry et al. 1995).

Additional collections examined. BRAZIL. Amazonas: Rio Juruá, Nov 1900, E.H.G. *Ule* 5013 (L-0160690, K-001205092). VENEZUELA. Amazonas: En la isla de Trapichote, Delta del Ventuari, [3°57'31.45"N, 67°12'7.45"W], alt. 125 m, 21 Apr 1942, L. Williams 14990 (paratypes: F-1189188, US-1833601).

Distribution and preliminary conservation status. Known from only three collections. The two from Venezuela are ~220 km apart in lowland rainforests of the upper Orinoco Basin and Río Casiquiare of western Amazonas. The Brazilian collection occurs at least 500 km to the south along the Rio Juruá (locality imprecise) in Amazonas. They occur in remote, pristine rainforest and their IUCN Red List Category presently should be Data Deficient given limited information of distribution and threats.

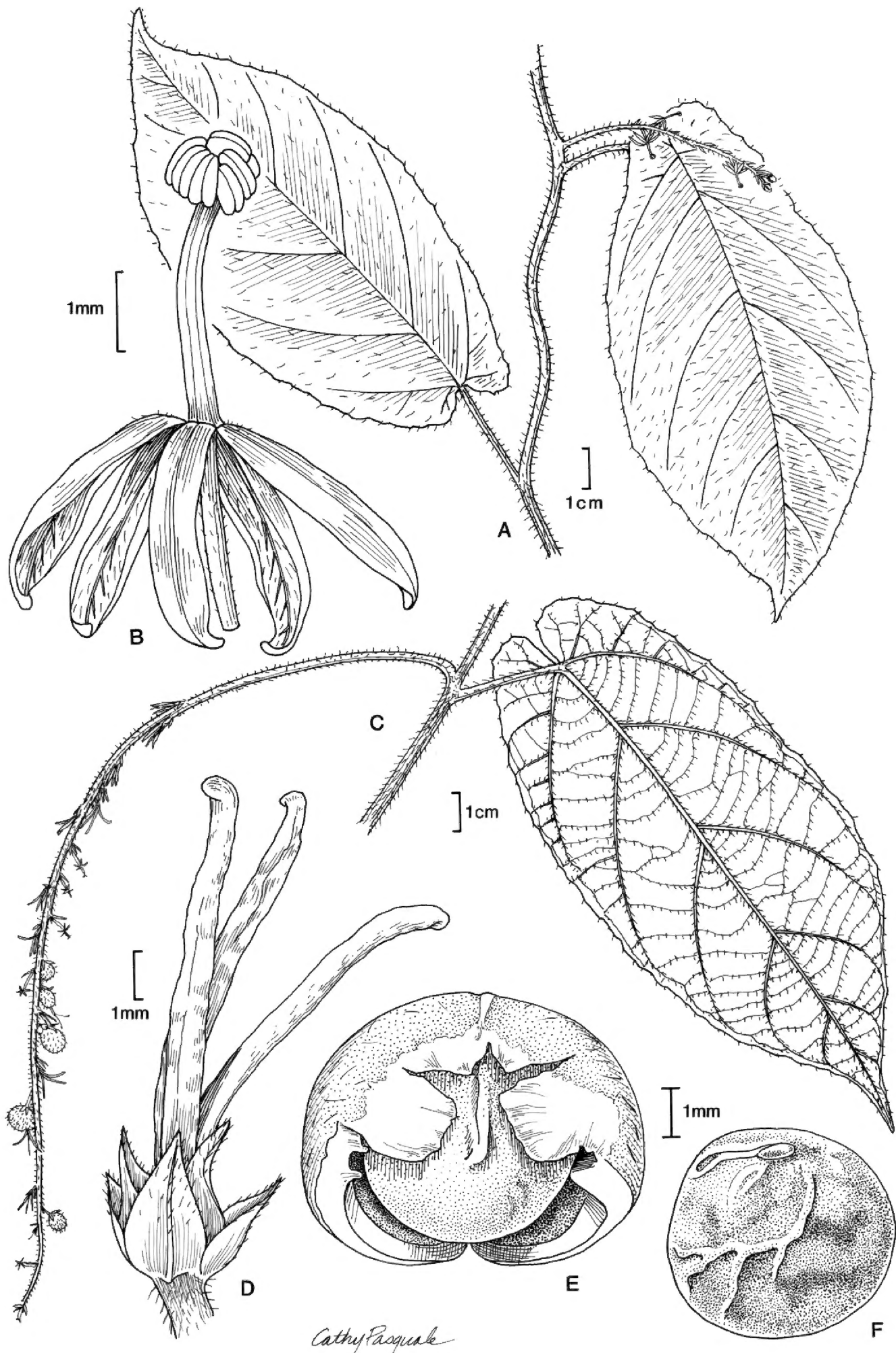


Figure 1. Illustration of *Monadelpha guayanensis*. **A** habit showing staminate inflorescence **B** staminate flower **C** habit showing infructescence **D** pistillate flower **E** mericarp of dehiscent capsule with enclosed seed **F** seed, lateral view with hilum at top. Sources: **A, B** based on *Stergios & Aymard 9182* (MO) **C–F** based on *Stergios & Aymard 9182* (NY). Illustration by Cathy Pasquale reproduced from Gillespie (1994b) with permission from the Missouri Botanical Garden Press.

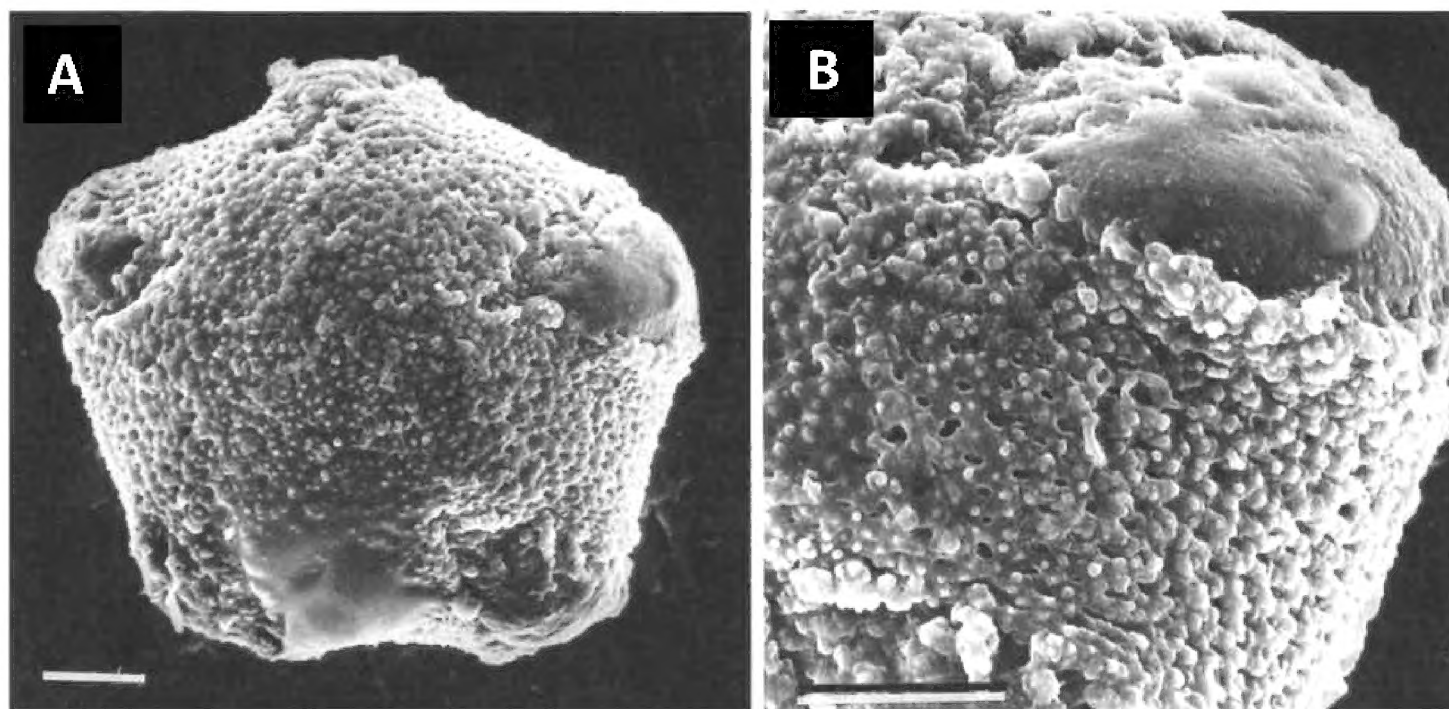


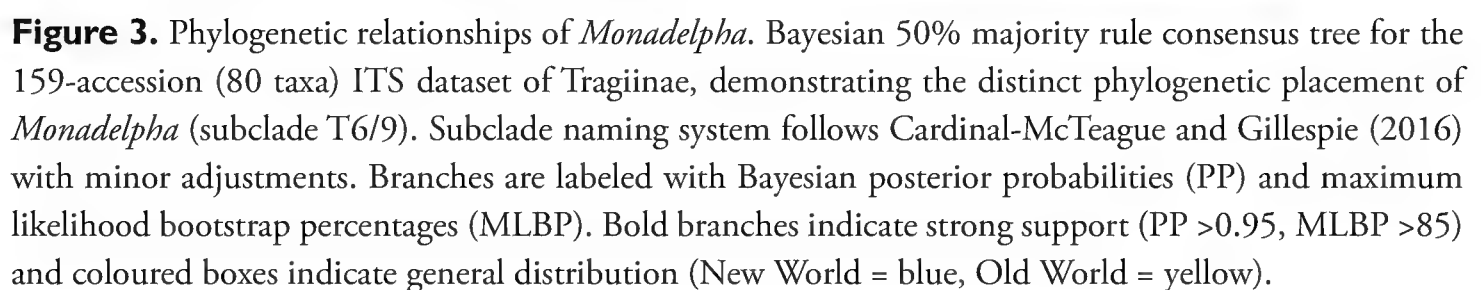
Figure 2. Pollen morphology of *Monadelphpha guayanensis* **A** SEM of pollen grain showing polar view with five colpi **B** closeup of mesocolpium and two colpi. Source: *Stergios & Aymard 9182* (MO). Figure reproduced from Gillespie (1994b) with permission from the Missouri Botanical Garden Press.

Notes. *Monadelphpha guayanensis* is newly reported here from Brazil based on one 1900 collection by E.H.G. Ule. Staminate inflorescences on this collection (L-0160690 sheet) are considerably longer than previously described, and are closer in length to the pistillate inflorescence. It appears that the staminate inflorescence on the holotype may be damaged and partly missing or possibly less mature. Leaf blades are more variable in size and shape than on the two Venezuelan collections, some blades being very similar, others larger and relatively broader.

Monadelphpha guayanensis has unisexual inflorescences and is likely monoecious (rather than dioecious). Although unisexual inflorescences are not found on the same branch, the type collection, *Stergios & Aymard 9182*, has inflorescences of both sexes, and is thus monoecious if one assumes branches originate from a single individual. Further collections are needed to confirm this character.

Key to Tragiinae in South America and Central America

- 1 Filaments absent or entirely connate into an elongate staminal column; pollen 4- or 5-colpate; inflorescences unisexual, racemose; staminate flowers with 5 sepals and 5 stamens **2**
- Filaments distinct or rarely partly connate; pollen 3-colpate, weakly 3-porate, or inaperturate; inflorescences bisexual (unisexual in *Gitara*), racemose or paniculate with a single branch; staminate flowers with 3–5 (6) sepals and (1) 2–40+ stamens **3**
- 2 Anthers in a dense cluster on an elongate \pm cylindrical staminal column; pollen 5-colpate; styles cylindrical, 6–10 mm long..... ***Monadelphpha***
- Anthers sessile; pollen 4-colpate; stigmas subsessile, broad... ***Tragia rubiginosa***



- 3 Inflorescences unisexual; dioecious, erect shrubs; anther connective with tuft of stinging hairs ***Gitara***
- Inflorescences bisexual with pistillate flowers basal; monocious vines, herbs, or subshrubs; anther connective lacking tuft of stinging hairs or present but minute **4**
- 4 Inflorescences racemose, with 1 (2) pistillate flower(s) at the basal 1 (–9) node(s) (*T. polyandra* with (1) 2–4 (5) flowers on a short basal branch); stamens (1) 2–5 (–22); staminate disc usually absent, if present comprising a single central structure; pollen exine intectate, baculate ***Tragia* (sect. *Tragia*)**
- Inflorescences consisting of a racemose staminate main axis and a single elongate basal branch bearing 5–30 pistillate flowers (branch short with (1) 2–4 flowers in *Zuckertia manuelii*); stamens 6–40+; staminate disc segmented or absent; pollen exine tectate, finely reticulate or foveolate-fossulate **5**
- 5 Staminate flowers with 3 (4) sepals, 5–10 disc segments, and 6–20 stamens; leaf blades 5–16 cm long, usually unlobed; pollen inaperturate; South America to Costa Rica ***Bia***
- Staminate flowers with 5 or 6 sepals, no disc, and 17–40+ stamens; leaf blades (7–) 12–25 cm long, unlobed to 3-lobed; pollen tricolpate; Mexico and Central America ***Zuckertia***

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Appendix I

Sources for ITS data used in phylogenetic analyses. Voucher data (country, collector, number, herbarium code) are provided, with new GenBank numbers in bold and beginning with MK and MW.

Outgroup: *Adenophaedra grandifolia* (Klotzsch) Müll.Arg. COSTA RICA • Valverde 48 (NY), **MK780909**. *Bernardia nicaraguensis* Standl. & L.O.Williams NICARAGUA • Stevens 30168 (MO), KP794419. *Caryodendron grandifolium* (Müll.Arg.) Pax ECUADOR • Korning 8502 (MO), KP794421. **Ingroup:** *Acidoton microphyllus* Urban DOMINICAN REPUBLIC • Liogier 14216 (NY), **MK780907**. *Acidoton urens* Sw. JAMAICA • Thorne 48242 (MO), KP794316. *Acidoton urens* Sw. JAMAICA • Webster 8184 (DAV), **MK780908**. *Bia alienata* Didr. BOLIVIA • Carretero 1237 (MO), KP794320. *Bia alienata* Didr. Paraguay • Pérez 352 (MO), KP794318. *Bia alienata* Didr. PARAGUAY • Stevens et al. 31232 (MO), **MK780928**. *Bia alienata* Didr. PARAGUAY • Zardini 11174 (MO), KP794319. *Bia fendleri* Müll.Arg. BOLIVIA • Beck 8253 (MO), KP794321. *Bia fendleri* Müll.Arg. PARAGUAY • Seidel and Herzog 7516 (DAV), **MK780930**. *Bia fendleri* Müll.Arg. PERU • Webster 23296 (DAV), **MK780929**. *Bia* cf. *lessertiana* BRAZIL • Noblick 3117 (DAV), **MK780931**. *Bia lessertiana* Baill. BRAZIL • Webster 25586 (DAV), **MK780932**. *Cnesmone javanica* Blume BANGLADESH • Huq 10189 (US), **MK780937**. *Cnesmone javanica* Blume THAILAND • Chamchumroon 2019 (L), KP794430. *Cnesmone javanica* Blume THAILAND • Larsen 44027 (MO), KP794427. *Cnesmone javanica* Blume THAILAND • Larsen 44147 (MO), KP794428. *Cnesmone laotica* (Gagnep.) Croizat THAILAND • van Beusekom 4154 (L), KP794431. *Cnesmone tonkinensis* (Gagnep.) Croizat VIETNAM • Gillespie 7406 (CAN), **MK780938**. *Ctenomeria capensis* (Thunb.) Harv. ex Sond. SOUTH AFRICA • Balkwill and Balkwill 10715 (MO), **MK780939**. *Ctenomeria capensis* (Thund.) Harv. ex Sond. SOUTH AFRICA • Hugo 2107 (MO), KP794322. *Gitara nicaraguensis* (Hemsl.) Card.-McTeag. & L.J.Gillespie BRAZIL • Berg et al. 729 (CAN), **MK780953**. *Gitara nicaraguensis* (Hemsl.) Card.-McTeag. & L.J.Gillespie ECUADOR • Korning 47437 (MO), KP794398.

Gitara nicaraguensis (Hemsl.) Card.-McTeag. & L.J.Gillespie NICARAGUA • Stevens 33392 (MO), **MK780954**. *Gitara nicaraguensis* (Hemsl.) Card.-McTeag. & L.J.Gillespie PANAMA • Ibañez 2038 (MO), KP794397. *Megistostigma peltatum* (J.J.Sm.) Croizat THAILAND • Maxwell 87-462 (L), **MK780958**. *Megistostigma yunnanense* Croizat THAILAND • Larsen 46354 (L), **MK780959**. *Monadelpha guayanensis* (L.J.Gillespie) L.J.Gillespie & Card.-McTeag. VENEZUELA • Williams 14990 (US-1833601), **MW264490**. *Pachystylidium hirsutum* (Blume) Pax & K.Hoffm. THAILAND • Keer 17893 (L), KP794408. *Platygyne hexandra* (Jacq.) Müll.Arg. CUBA • Acevedo-Rodríguez 5566 (NY), KP794317. *Platygyne hexandra* (Jacq.) Müll.Arg. CUBA • HAJB 81903 (MICH), **MK780963**. *Platygyne hexandra* (Jacq.) Müll.Arg. CUBA • HAJB 81961 (MICH), **MK780964**. *Platygyne parvifolia* Alain CUBA • HAJB 81826 (MICH), **MK780965**. *Sphaerostylis perrieri* Leandri MADAGASCAR • Gillespie 10738 (CAN), KP794413. *Sphaerostylis perrieri* Leandri MADAGASCAR • Gillespie 10739 (CAN), KP794414. *Sphaerostylis perrieri* Leandri MADAGASCAR • Gillespie 10742 (CAN), KP794415. *Sphaerostylis perrieri* Leandri MADAGASCAR • Labat 3441 (MO), KP794412. *Tragia* aff. *furialis* TANZANIA • Lovett 3707 (MO), KP794344. *Tragia* aff. *pacifica* EL SALVADOR • Sandoval 1777 (MO), KP794388. *Tragia amblyodonta* (Müll. Arg.) Pax & K.Hoffm. USA • B.L. 98-372 (MO), KP794376. *Tragia arabica* (Müll. Arg.) Baill. ex Prain ETHIOPIA • Burger 3592 (US), **MK780910**. *Tragia arnhemica* P.I.Forst. AUSTRALIA • Brennan 2016 (DNA), KP794410. *Tragia arnhemica* P.I.Forst. AUSTRALIA • Russel-Smith 5235 (DNA), KP794409. *Tragia baroniana* Prain MADAGASCAR • Gillespie et al. 10723 (CAN), **MK780911**. *Tragia baroniana* Prain MADAGASCAR • Gillespie et al. 10748 (CAN), **MK780912**. *Tragia benthamii* Baker TANZANIA • Bidgood 4648 (MO), KP794328. *Tragia betonicifolia* Nutt. USA • Smith 3940 (MO), KP794364. *Tragia betonicifolia* Nutt. USA • Summers 9529 (MO), KP794363. *Tragia brevipes* Pax TANZANIA • Bidgood 4686 (MO), KP794325. *Tragia brevipes* Pax UGANDA • Rwaburindore 4488 (MO), KP794329. *Tragia caperonoides* Pax & K. Hoffm. PARAGUAY • Zardini and Gamarra 59470 (MO), **MK780967**. *Tragia cearensis* Pax & K.Hoffm. BRAZIL • Medeiros et al. 512 (R), **MK780968**. *Tragia cearensis* Pax & K.Hoffm. BRAZIL • Medeiros et al. 523 (R), **MK780969**. *Tragia cearensis* Pax & K.Hoffm. BRAZIL • Medeiros et al. 525 (R), **MK780970**. *Tragia* cf. *bahiensis* PARAGUAY • Zardini 52840 (MO), KP794378. *Tragia* cf. *cocculifolia* MADAGASCAR • McPherson and van der Werff 16441 (CAN), **MK780913**. *Tragia* cf. *hieronymi* BOLIVIA • Mendoza 474 (NY), **MK780975**. *Tragia* cf. *pacifica* MEXICO • Castrejón 753 (MO), KP794392. *Tragia* cf. *petiolaris* UGANDA • ATBP 624 (MO), KP794351. *Tragia* cf. *pohlii* BRAZIL • Irwin 5514 (NY), **MK780971**. *Tragia* cf. *yucatanensis* MEXICO • Álvarez 6623 (MO), KP794383. *Tragia* cf. *yucatanensis* GUATEMALA • Wallnöfer 5898 (MO), KP794381. *Tragia chlorocaulon* Baill. BRAZIL • Dawson 15122 (MO), KP794390. *Tragia chlorocaulon* Baill. BRAZIL • Irwin 15858 (MO), KP794391. *Tragia chlorocaulon* Baill. BRAZIL • Medeiros et al. 503 (R), **MK780973**. *Tragia cocculifolia* Prain MADAGASCAR • Razanatsoa 250 (MO), KP794331. *Tragia cordata* Michx. USA • McDaniel 28890 (MO), KP794395. *Tragia cordata* Michx. USA • Thomas 171769 (MO), KP794396. *Tragia cordata* Michx. USA • Thomas 76208 (CAN), KP794394.

Tragia dinteri Pax NAMIBIA • Seydel 2830 (L), **MK780914**. *Tragia dioica* Sond. NAMIBIA • Seydel 5539 (MO), KP794335. *Tragia dioica* Sond. NAMIBIA • Volk 6173 (MO), KP794332. *Tragia durbanensis* Kuntze SOUTH AFRICA • Balsinhas 3095 (MO), KP794333. *Tragia finalis* P.I.Forst. AUSTRALIA • Gillespie 7390 (CAN), KP794411. *Tragia furialis* Bojer ex Prain MADAGASCAR • Gillespie 10648 (CAN), KP794342. *Tragia furialis* Bojer ex Prain MADAGASCAR • Gillespie 10700 (CAN), **MK780917**. *Tragia furialis* Bojer ex Prain MADAGASCAR • Nusbaumer 2725 (MO), KP794343. *Tragia furialis* Bojer ex Prain MAYOTTE • Barthlet 171 (MO), KP794341. *Tragia furialis* Bojer ex Prain TANZANIA • Kayombo 5098 (MO), KP794340. *Tragia geraniifolia* Klotzsch ex Baill. ARGENTINA • Krapovickas 20133 (MO), KP794368. *Tragia geraniifolia* Klotzsch ex Baill. PARAGUAY • Peña-Chocarro 2240 (MO), KP794370. *Tragia giardelliae* M.M.Gutiérrez & M.E.Múlgura ARGENTINA • Guaglianone 2994 (MO), KP794360. *Tragia giardelliae* M.M.Gutiérrez & M.E.Múlgura ARGENTINA • Múlgura 399 (NY), **MK780974**. *Tragia hildebrandtii* Müll.Arg. TANZANIA • Abdallah 96/157 (MO), KP794355. *Tragia jonesii* Radcl.-Sm. & Govaerts MEXICO • Felger 85-909 (MO), KP794377. *Tragia laciniata* (Torr.) Müll.Arg. MEXICO • Yatskievych 11-59 (MO), **MK780976**. *Tragia laminularis* Müll.Arg. CÔTE D'IVOIRE • Gautier-Béguin 592 (MO), KP794349. *Tragia laminularis* Müll.Arg. CÔTE D'IVOIRE • Gautier-Béguin 959 (MO), KP794348. *Tragia melochioides* Griseb. BOLIVIA • Coca 50 (MO), KP794373. *Tragia melochioides* Griseb. BOLIVIA • Lozano 1784 (MO), KP794372. *Tragia melochioides* Griseb. URUGUAY • Denham et al. 300 (SI), **MK780978**. *Tragia mexicana* Müll.Arg. BELIZE • Peña 1029 (MO), KP794393. *Tragia minor* Sond. SOUTH AFRICA • Balsinhas 3631 (MO), KP794338. *Tragia nepetifolia* Cav. MEXICO • García 446 (MO), KP794366. *Tragia novae-hollandiae* Müll.Arg. AUSTRALIA • Bower S3 (CAN), **MK780960**. *Tragia novae-hollandiae* Müll.Arg. AUSTRALIA • Gillespie 7394 (CAN), KP794417. *Tragia okanyua* Pax BOTSWANA • Long 386 (MO), KP794336. *Tragia okanyua* Pax ZAMBIA • Schmidt 2323 (MO), KP794337. *Tragia pacifica* McVaugh EL SALVADOR • Rosales 672 (MO), KP794389. *Tragia paxii* Lourteig & O'Donnell ARGENTINA • Johnson 920 (MO), KP794380. *Tragia paxii* Lourteig & O'Donnell ARGENTINA • Múlgura 2307 (MO), KP794379. *Tragia petiolaris* Radcl.-Sm. TANZANIA • Greenway and Polhill 11556 (L), **MK780920**. *Tragia petiolaris* Radcl.-Sm. TANZANIA • Kuchar 25067 (MO), KP794354. *Tragia pinnata* (Poir.) A.Juss. ARGENTINA • Tressens 2202 (MO), KP794369. *Tragia plukenetii* Radcl.-Sm. ETHIOPIA • Burger 3768 (US), **MK780919**. *Tragia plukenetii* Radcl.-Sm. UGANDA • Rwaburindore 5745 (MO), KP794356. *Tragia pohlii* Müll.Arg. BRAZIL • Eiten 4836 (UBC), **MK780979**. *Tragia polyandra* Vell. ARGENTINA • Múlgura 2061 (MO), KP794375. *Tragia preussii* Pax CAMEROON • Nkongmeneck 1400 (MO), KP794352. *Tragia pungens* (Forssk.) Müll. Arg. ETHIOPIA • De Wilde 6406 (MO), KP794327. *Tragia pungens* (Forssk.) Müll.Arg. SOMALIA • Bally 16026 (MO), KP794326. *Tragia pungens* (Forssk.) Müll.Arg. YEMEN • Spellenberg 7547 (L), **MK780921**. *Tragia ramosa* Torr. USA • Hill 18339 (MO), KP794371. *Tragia ramosa* Torr. USA • Ricketson 4600 (MO), KP794367. *Tragia rogersii* Prain SOUTH AFRICA • Ellery 92/96 (MO), KP794339. *Tragia rupestris* Sond. SOUTH AFRICA • Venter 9666 (MO), KP794334. *Tragia saxicola* Small USA • Conell

40056 (MO), KP794386. *Tragia saxicola* Small USA • Kral 51842 (MO), KP794387. *Tragia smallii* Shinnars USA • McDaniel 28193 (MO), KP794401. *Tragia smallii* Shinnars USA • McDaniel 28698 (MO), KP794402. *Tragia* sp. *Ratiga* EL SALVADOR • Rodriguez and Tejada 2150 (MO), **MK780980**. *Tragia* sp. *Tagira* ZAMBIA • Harder and Bingham 2582 (CAN), **MK780923**. *Tragia spathulata* Benth. TOGO • Breteler 7083 (MO), KP794350. *Tragia subsessilis* Pax TANZANIA • Vollesen 96/44 (MO), KP794345. *Tragia tenuifolia* Benth. CÔTE D'IVOIRE • Gautier 2266 (MO), KP794353. *Tragia tiverneana* Leandri MADAGASCAR • Hanitrarivo 325 (CAN), **MK780925**. *Tragia tiverneana* Leandri MADAGASCAR • Rakotozafy et al. 55 (CAN), **MK780924**. *Tragia tristis* Müll.Arg. BRAZIL • Anderson 9117 (NY), **MK780981**. *Tragia uberbana* Müll.Arg. ARGENTINA • Zuloaga 5785 (MO), KP794374. *Tragia urens* L. USA • Abbott 22604 (MO), **MK780957**. *Tragia urens* L. USA • Anderson 7188 (MO), KP794407. *Tragia urens* L. USA • Kral 41155 (MO), KP794406. *Tragia urens* L. USA • Mayfield 2006 (MO), **MK780956**. *Tragia urens* L. USA • Thomas 100075 (MO), KP794404. *Tragia urens* L. USA • Thomas 124328 (MO), KP794405. *Tragia urens* L. USA • Thomas 55051 (CAN), KP794403. *Tragia urticifolia* Michx. USA • Thomas 97259 (CAN), KP794365. *Tragia volubilis* L. BOLIVIA • Peñarando et al. 651 (MO), **MK780987**. *Tragia volubilis* L. BOLIVIA • Villalobos et al. 1251 (MO), **MK780988**. *Tragia volubilis* L. BRAZIL • Medeiros and Cardinal-McTeague 556 (R), **MK780984**. *Tragia volubilis* L. BRAZIL • Medeiros and Cardinal-McTeague 563 (R), **MK780985**. *Tragia volubilis* L. BRAZIL • Medeiros et al. 490 (R), **MK780983**. *Tragia volubilis* L. BRAZIL • Medeiros et al. 499 (R), **MK780982**. *Tragia volubilis* L. COSTA RICA • Hammel 19108 (MO), KP794362. *Tragia volubilis* L. NICARAGUA • Stevens 29658 (MO), KP794361. *Tragia volubilis* L. NICARAGUA • Stevens and Montiel 34954 (MO), **MK780986**. *Tragia yucatanensis* Millsp. GUATEMALA • Christenhusz 5678 (MO), KP794384. *Tragia yucatanensis* Millsp. MEXICO • Alvarez 4398 (MO), KP794382. *Tragia yucatanensis* Millsp. MEXICO • Lira 420 (MO), KP794385. *Tragiella anomala* (Prain) Pax & K.Hoffm. TANZANIA • Luke 11120 (MO), KP794324. *Tragiella anomala* (Prain) Pax & K.Hoffm. TANZANIA • Mwasumbi 16202 (MO), KP794323. *Tragiella friesiana* (Prain) Pax & K.Hoffm. ZAMBIA • Nkhoma 73 (MO), KP794346. *Tragiella friesiana* (Prain) Pax & K.Hoffm. ZAMBIA • Nkhoma 74 (MO), KP794347. *Tragiella natalensis* (Sond.) Pax & K.Hoffm. TANZANIA • Massawe 519 (MO), KP794330. *Zuckertia cordata* Baill. COSTA RICA • González 1045 (MO), KP794399. *Zuckertia cordata* Baill. MEXICO • Calzada 1544 (MO), KP794400. *Zuckertia manuelii* (V.W.Steinm. & Ram.-Amezcuca) Card.-McTeag. & L.J.Gillespie MEXICO • Steinmann et al. 6303 (CAN), **MK780989**.